



THE UNIVERSITY *of* EDINBURGH

Edinburgh Research Explorer

The mesic savannas of the Bateke Plateau: carbon stocks and floristic composition

Citation for published version:

Nieto-quintano, P, Mitchard, ETA, Odende, R, Batsa Mouwembe, MA, Rayden, T & Ryan, CM 2018, 'The mesic savannas of the Bateke Plateau: carbon stocks and floristic composition', *Biotropica*.
<https://doi.org/10.1111/btp.12606>

Digital Object Identifier (DOI):

[10.1111/btp.12606](https://doi.org/10.1111/btp.12606)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Publisher's PDF, also known as Version of record

Published In:

Biotropica

General rights

Copyright for the publications made accessible via the Edinburgh Research Explorer is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

The University of Edinburgh has made every reasonable effort to ensure that Edinburgh Research Explorer content complies with UK legislation. If you believe that the public display of this file breaches copyright please contact openaccess@ed.ac.uk providing details, and we will remove access to the work immediately and investigate your claim.



The mesic savannas of the Bateke Plateau: carbon stocks and floristic composition

Paula Nieto-Quintano^{1,5} , Edward T. A. Mitchard¹, Roland Odende², Marcelle A. Batsa Mouwembe³, Tim Rayden⁴, and Casey M. Ryan¹

¹ School of GeoSciences, University of Edinburgh, Crew Building, Edinburgh EH9 3FF, UK

² Laboratoire de botanique et d'écologie, Faculté des Sciences et Techniques, Université Marien Ngouabi, BP 69, Brazzaville, Congo

³ Ecole Nationale Supérieure d'Agronomie et de Foresterie, Université Marien Ngouabi, BP 69, Brazzaville, Congo

⁴ Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, New York, USA

ABSTRACT

The Bateke Plateau in the Republic of Congo is one of the last frontiers for ecology, with little known about its floristics and physiognomy. Despite occupying 89,800 km² and its importance for local livelihoods, its ecology and ecosystem functions are poorly understood. Situated on Kalahari sands, the Bateke has a complex evolutionary history, mainly isolated from other savannas for much of its past, with currently unresolved ecological implications. Here, we assess the biomass and floristic diversity of this savanna. We established four 25-ha permanent sample plots at two savanna sites; inventoried all trees; assessed biomass and species composition of shrubs, forbs and grasses; and characterized the soils. Total plant carbon stocks (aboveground and belowground) were only 6.5 ± 0.3 MgC/ha, despite precipitation of 1600 mm/yr. Over half the biomass was grass, with the remainder divided between trees and shrubs. The carbon stock of the system is mostly contained in the top layer of the soil (16.7 ± 0.9 MgC/ha in 0–20 cm depth). We identified 49 plant species (4 trees, 13 shrubs, 4 sedges, 17 forbs, and 11 grass species), with an average species richness of 23 per plot. There is tree hyperdominance of *Hymenocardia acida* (Phyllanthaceae) and a richer herbaceous species composition dominated by *Loudezia simplex* and *Hyparrhenia diplandra*. The low carbon stocks and tree biodiversity, compared to other African savannas, are surprising considering the high rainfall. We speculate it is due to low nutrient soils, high fire frequency, and the effect of a temporally variable and restricted connection to the main southern African savanna complex.

Abstract in French is available with online material.

Key words: Bateke Plateau; carbon stocks; Republic of Congo; savanna; species composition.

THE BATEKE PLATEAU IS A SAVANNA-COVERED PLATEAU LOCATED MAINLY IN THE SOUTHERN REPUBLIC OF CONGO, but also extending into the east of Gabon and the southwest of Democratic Republic of Congo (DRC), and with an area of approximately 89,800 km² (Fig. 1). It comprises five different savanna plateaus (Koukouya, Djambala, Nsa, Ngo, and Mbé/Batéké), with an elevation that ranges from 259 to 872 m (mean of 545 m), each separated by deep valleys (Descoigns 1960, Congo Basin Forest Partnership, 2006). The landscape is located on the northern part of the Kalahari sands, an ancient sand dune system (Haddon 2000), with soils that are mainly deep, sandy in texture and ferralitic (Schwartz & Namri 2002), providing rapid drainage. There are also some podzols in lower areas (Schwartz 1988). This area has a tropical transitional climate, characterized by an average annual rainfall of 1500–1800 mm (obtained from Harris *et al.* 2014). There is a main dry season from June to September and a short dry season in January and February (Walters 2010b). The Bateke Plateau has historically low human population densities, around 0.2 inhabitants/

km² (Congo basin forest partnership 2006). Batéké populations mainly practice subsistence agriculture, gathering, fishing, and hunting (Walters 2010a, Rayden *et al.* 2014). Agro-economic activities, charcoal production, logging, hunting, and bushfires have widely impacted this landscape, driven by the demand from the large capital cities of Brazzaville and Kinshasa (populations of 1.8 and 9.5 million, respectively) (Hoare 2007).

The vegetation of the Bateke Plateau is predominantly a mosaic of woody savanna and grasslands, with patches of closed canopy forest, the latter confined to rivers and valley floors, pockets at the top of hills, and surrounding settlements, where there is greater water availability and protection from fire (Duvigneaud 1953b). The wooded savanna is dominated by an open canopy of *Hymenocardia acida* Tul. (Phyllanthaceae) and *Annona senegalensis* Pers. (Annonaceae) trees, with an understory of grasses and locally endemic forbs (Walters 2012). The grasslands are typically dominated by *Loudezia simplex* and *Hyparrhenia diplandra* (Duvigneaud 1953b).

The Bateke Plateau intrudes into the Congo Basin rainforest and has a precipitation clearly suitable for closed canopy forest establishment. Here, savanna and forest coexist under the same

Received 24 May 2018; revision accepted 26 July 2018.

⁵Corresponding author; e-mail: paula.nieto@ed.ac.uk

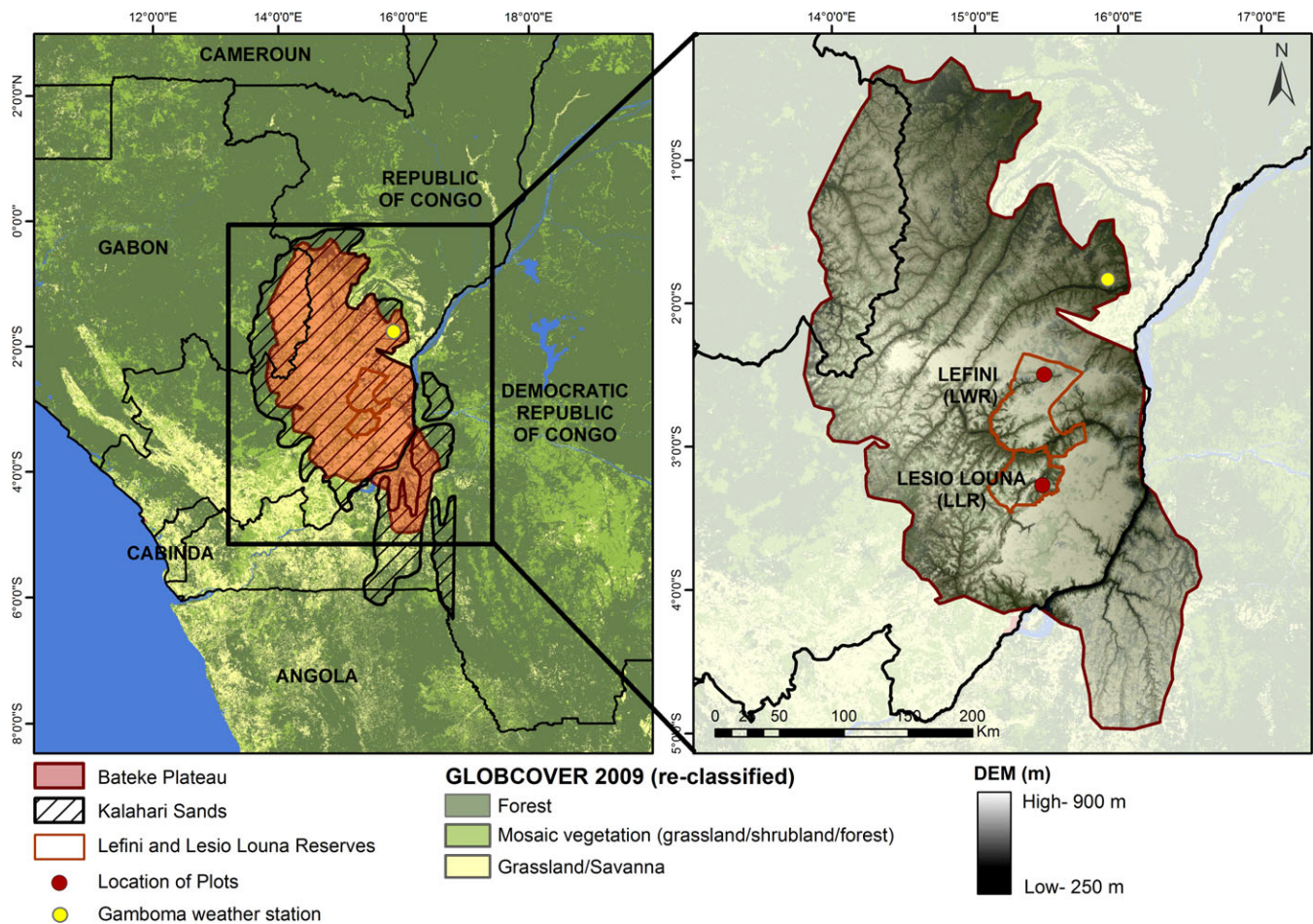


FIGURE 1. Map of the study area, the Bateke Plateau, located mainly in the Republic of Congo. The left-hand map shows the extent of the Bateke Plateau (red), the Kalahari sands (dashed), and the weather station of Gamboma used for the analysis of the temperature and precipitation data (yellow dot). The right-hand panel shows the location of the Lefini and Lesio Louna reserves, where the sampling plots were placed (red dots), over a Digital Elevation Model (DEM) and the land use cover (GlobCover 2009, reclassified).

climatic and edaphic conditions with sharp transitions (Schwartz *et al.* 1995). This has made it problematic to define the origin of this savanna, with conflicting hypotheses as to the lack of tree cover, which have important consequences for its conservation (Veldman *et al.* 2014, 2015, Bond & Zaloumis 2016). Some authors (Aubreville 1949, Duvigneaud 1953b, Elenga *et al.* 1994) have suggested an anthropogenic origin, caused by the arrival of human populations. Conversely, the weight of recent evidence supports an origin caused by arid events in the past, though humans could have played a role (Koechlin 1960, Aubréville 1962, Foresta 1990, Elenga *et al.* 1994, Schwartz *et al.* 1995, Vincens *et al.* 1999, Oslisly *et al.* 2013). The recent climatic history of the region is complex. There is evidence of a humid period with mainly forests covering the region from 40,000 to 24,000 years BP, followed by a drier period from 24,000 to 12,000 years BP when herbaceous communities expanded (Dechamps *et al.* 1988, Schwartz 1988, Elenga *et al.* 1994, Schwartz *et al.* 1995). From 12,000 years BP onwards, humid conditions encouraged new forest development (Dechamps *et al.* 1988, Elenga *et al.* 1994),

supported by studies suggesting that, as recently as 4000-3500 years BP, the Bateke Plateau was forested (Dechamps *et al.* 1988, Schwartz *et al.* 1995, Vincens *et al.* 1999). These forests were likely replaced by open grasslands around 3000 years BP, when a major arid event occurred with greater seasonality, causing extension of grasses (Elenga *et al.* 1994, Schwartz *et al.* 1995, Vincens *et al.* 1999, Maley 2001), and coincident with the arrival of increased human populations (Schwartz 1992). However, even during the most humid episodes of the past 40,000 years, there is evidence that some savanna still existed in the area (Dechamps *et al.* 1988, Vincens *et al.* 1999).

The Bateke belongs to the Guineo-Congolian center of endemism (White 1983), with most of the Bateke being in the Western Congolian forest-savanna mosaic ecoregion (Olson *et al.* 2001). These savannas have been fairly isolated from other savanna formations, especially from West Africa by the Congo Basin rainforest. In the Guineo-Congolian region (White 1979) and in southern Kalahari areas, endemism is high (Walters *et al.* 2006), with many sand-adapted and pyrophytic species. This

suggests potential for endemism in the Bateke, and indeed this is supported by recent findings (Bamps 2013). In Gabon, there have been recent reports of more than 30 new plant records from savannas, and six globally rare species restricted to Kalahari sands or moist savannas (Walters *et al.* 2006, van der Maesen & Walters 2011), and in South Congo, Koechlin (1960) found 12% endemic species. However, Bateke savannas were considered by White (1983) as secondary with some being edaphic and by Schwartz *et al.* (1995) as inclusive or edaphic, and original, without equivalent in the past. The theory of Bateke savannas being secondary would contradict potential endemism, as secondary savannas tend to have lower plant species richness and absence of geoxyllic suffrutices (Zaloumis & Bond 2016). Plant species with a geoxyllic suffrutex growth form are plants with large woody underground structures and short-lived aerial shoots, with a high capacity to resprout stimulated by fire, thus providing an alternative escape from fire (White 1977). They are mainly endemic to the Kalahari sands of the Zambezian region and occur almost exclusively in higher rainfall savannas with frequent fires (White 1977, 1979, Revermann *et al.* 2017).

There is evidence from charcoal that fires have occurred in the Bateke since 2100 BP, and almost certainly they occurred frequently far further back in time (Schwartz 1988, Walters 2012). Nowadays, fires are mostly anthropogenic, occurring mainly in the dry season for hunting and gathering (Walters 2010a, 2012). Frequent fires, fueled by the continuous layer of grasses, have unclear effects on species richness (Higgins *et al.* 2000, Smith *et al.* 2013) and probably encourage specialization (Walters *et al.* 2006). Herbivore densities are low and do not cause much disturbance due to historic and current hunting, though there probably were once high herbivore densities that could have shaped the landscape (Walters 2010b).

BIOMASS STOCKS AND BOTANICAL STUDIES IN THE BATEKE PLATEAU.—Savannas cover around half of the African continent (Menaut 1983), but despite their importance to the global carbon cycle, current knowledge of African savanna biomass stocks and floristic diversity is limited (Hall & Scurlock 1991), especially in the understudied ecosystems of the Bateke Plateau.

We searched and collated the published and gray literature of the Bateke to provide a first comprehensive review of the biomass stocks in the Plateau and found eight studies that have previously quantified some aspects of biomass stocks of these savannas (Makany 1973, Apani 1990, Schwartz & Namri 2002, Yoka *et al.* 2010, 2013, Gigaud 2012, Lokegna 2015, Ifo 2017). These values are in general low for African savannas. There have been still fewer estimates of soil carbon stocks in the Batéké Plateau (Namri 1996, Schwartz & Namri 2002, Ifo 2017). The spatial scale of all these studies is restricted, and none have assessed all ecosystem carbon storage elements together, limiting their ability to provide understanding of the system.

We have better knowledge of the plant species of the region, with floristic inventories of Gabon (Aubréville 1961) and DRC (Robyns 1949), and a Checklist for Gabon (Sosef 2006). In RoC, there is a published inventory for the vascular flora of the Republic

of Congo (Sita and Moutsambote (1988)), which provides a list of 4397 species (198 families and 1338 genera), but with the vast majority being forest species and no indication of their distribution. This inventory has been slightly updated since then, with 84 species added by Champluvier and Dowsett-Lemaire (1999), and 64 by Lachenaud (2009). More usefully, there is an illustrated list of plants of the Lesio Louna and Lefini reserves, which are major reserves covering 6% of the Bateke Plateau, that list 457 species belonging to 119 families (Nsongola *et al.* 2006). Some old botanical studies in French of this landscape also exist, but they are limited to the South of the Bateke (Koechlin 1960, Descoigns 1972), the Cuvette region (Descoigns 1960, Yoka *et al.* 2013), and the Teke Plateau (Makany 1973, Apani 1990), and in more recent some masters' theses (Lokegna 2015, Mampouya 2015). However, all these studies are limited in scope, contributing to the Republic of Congo being one of the botanically least known and inventoried countries in tropical Africa (Lachenaud 2009, Sosef *et al.* 2017).

Due to the lack of basic data on this ecosystem, it is difficult to understand its function, conservation value, and the transformations it could undergo with climate change and management changes. Our main objective was to characterize the structure of the vegetation and floristic diversity of the Bateke Plateau using data collected from four very large (25-ha) inventory plots, located within two protected areas and designed as a long-term fire experiment. Our research questions were as follows: (1) What is the carbon storage of our two woody savanna study sites, and how is it distributed between vegetation and the soil? (2) What is the species diversity of the study sites, and how does diversity vary by plant life form type? (3) Can we explain the structure of these savannas in the context its biogeographical history and human influence?

Due to frequent fires and intermediate rainfall, we expected these savannas to have a low tree biomass but higher grass biomass and understory diversity, with the presence of pyrophytes and geoxyllic suffrutex species. Moreover, if these savannas are ancient as recent evidence suggest, with a fluctuating savanna/forest cover for at least past 40,000 years, and because of its geographical position, we would anticipate high plant and forb diversity, presence of geoxyllic suffrutex, and some endemism. We would expect floristic similarities with the southern savannas due to the Kalahari sands acting as a corridor.

Overall, we provide a baseline biomass and diversity inventory for these savannas that we hope will be useful to other scientists interested in their structure and function, and assist with their management and conservation.

METHODS

SITE DESCRIPTION.—We conducted the study in two protected areas in the Bateke Plateau, the Lefini and the Lesio Louna reserves (Fig. 1), situated about 160 and 110 km north of Brazzaville, respectively. These sites have a precipitation of 1627 to 1966 mm/yr and a mean annual temperature of approximately 25°C (all calculated for the period 1996–2016 from data of Climate Research Unit (CRU) for the station of Gamboma (Harris *et al.* 2014), see

Fig. 1 for location). The Lefini Wildlife Reserve (LWR) has a total area of 5010 km² (IUCN & UNEP 2015) and was established in 1951 as a hunting reserve. The Lesio Louna Reserve (LLR) has a total area of 1730 km² and was established in 1993 as a sanctuary for the reintroduction of orphan gorillas by the Aspinall Foundation and later as a Natural Reserve in 1999. Both reserves are listed as IUCN Category IV and aim to maintain, conserve, and restore species and habitat (IUCN & UNEP 2015). They feature typical Bateke habitats: rolling hills studding a plateau dissected by river valleys, with open savanna dominating, and with forest patches around rivers and on the top of hills.

CARBON STOCK ASSESSMENT.—We established four 25-ha permanent sample plots (500 m × 500 m) in the savanna, two in each protected area, in the year 2015 as part of a long-term fire experiment (plots LWR1 and LWR2 in Lefini and plots LLR1 and LLR2 in Lesio Louna). The plots were not randomly located, selected to be in wooded savanna, easily reachable by foot from research camps, and sufficiently large to encompass much of the natural variability of the savannas. All four plots were located with one edge running about 30 m away from the edge of closed canopy forest, associated with nearby rivers. Data collection took place in 2015 in the beginning of the dry season (May/June) for plots LWR2 and LLR1 and in the end of the dry season (September/October) for plots LWR1 and LLR2.

In these plots, we inventoried all living trees with a diameter at breast height (dbh) greater than 10 cm, recording: species, dbh, height, status (alive/dead, standing/fallen, and broken), and spatial location (by GPS). Dbh was measured at 1.3 m height aboveground, and if the tree forked below this, each stem was measured independently and treated as different trees. Trees were identified to species level by Roland Odende, and their height was estimated using a Nikon Forestry Pro Laser.

For the estimation of the aboveground biomass (AGB) from these measurements, we used the generic pan-tropical allometric equation from Chave *et al.*, (2014) with wood density obtained from the Wood Density Database (Chave *et al.* 2009, Zanne *et al.* 2009) based on the species determination. This was considered the most appropriate for the study site as there are no locally defined allometric equations for this location. As height was estimated individually on the ground for every tree, there was no need to use diameter measurements to estimate tree height through a locally derived or regional relationship. However, we did compare dbh and height values in order to test the strength of this relationship in this ecosystem and to develop a model for use by others. Belowground tree biomass (BGB) was not measured in the field, but estimated using a root-to-shoot ratio (R:S = 0.42) described by Ryan *et al.* (2011) for miombo woodlands. We consider this equation was appropriate as the trees are subject to similar ecological pressure and constraints, and due to the absence of a local equation or one for Central African savannas.

To survey grasses and saplings/shrubs, the latter defined as woody plants with a dbh < 10 cm and with a diameter at 10 cm aboveground (D_{10}) greater than 1 cm, 16 permanent circular subplots with a radius of 4 m (50.3 m²) were established within

each plot, on every 100 m vertex, as shown in Fig. 2. In these subplots, saplings were tagged; measured (D_{10}) using a calliper, height, and dbh where applicable; and identified to species level. To estimate the biomass of the saplings (stems and roots), the allometric equations from Ryan *et al.* (2011) were applied for saplings with dbh < 5 cm.

$$SBs = 0.0007645 * D_{10}^2 + 0.004645 * D_{10} + 0.03876 \quad (1)$$

$$SBr = 0.001784 * D_{10}^2 + 0.0001413 * D_{10} + 0.15839 \quad (2)$$

where, SBs and SBr is the stem and root wet sapling biomass in kg, respectively. This was converted to biomass Mg/ha using the dry mass fraction (DMF) of 0.61 determined in the same study. For saplings with $D_{10} \geq 5$ cm and dbh < 10 cm, the Chave *et al.* (2014) Equation 1 was used for the AGB, and the ratio R: S = 0.42 for roots.

Grass biomass was measured using a disc pasture meter (DPM) (Bransby & Tainton 1977, Dörgeleh 2002), by taking four measurements at each subplot (therefore 64 measurements per 25-ha plot). The DPM was calibrated in each plot before its use. In order to perform this calibration, all the grass under the DPM was cut and weighed (wet weight). A subsample of grass was weighed, then dried to the point of no further weight loss, and re-weighed in order to determine dry mass based on percentage moisture loss from the samples. The relationship between mean disc settling heights (cm) and grass biomass per quadrat was determined separately for each plot using linear regression (linear calibration curve, $N = 35$ –40 for each plot, $r^2 = 0.35$ –0.75). BGB was not measured in the field, but it was estimated using the ratio calculated by Apani (1990) for grasses in the Teke Plateau (R:S = 2.5).

Biomass was converted into carbon stocks using a conversion factor of 0.47 (Ryan *et al.* 2011) for woody plants and 0.42 for grasses (Ryan 2009). All biomass values are given in metric tonnes of carbon per ha (MgC/ha).

SOIL ANALYSIS.—Soil analysis was performed in Plot LWR2 (Lefini) and LLR1 (Lesio Louna), by taking two soil samples (4 m apart) in each subplot located in the transects numbered 2 and 4 (Fig. 2), at two different horizons, h0 (0–5 cm) and h1 (5–20 cm), giving 32 soils samples per plot. Samples were dried, sieved, and analyzed in the physiochemical laboratory of the Institut de Recherche en Sciences Exactes et Naturelles (IRSEN) at Pointe-Noire, in order to determine total organic carbon, nitrogen content, and bulk density (measured with a cylinder core to assess the volume of the soil and determine the weight after drying, (Blake & Hartge 1986) (Batsa *et al.* (2017).

SPECIES COMPOSITION.—We performed a survey of the floristic composition by identifying all plant species within the subplots (presence/absence), first *in situ*, and where not possible samples were taken to the National Herbarium of IRSEN for identification, as described in Odende (2016). For six species, the identification was only possible to genus level. For the species

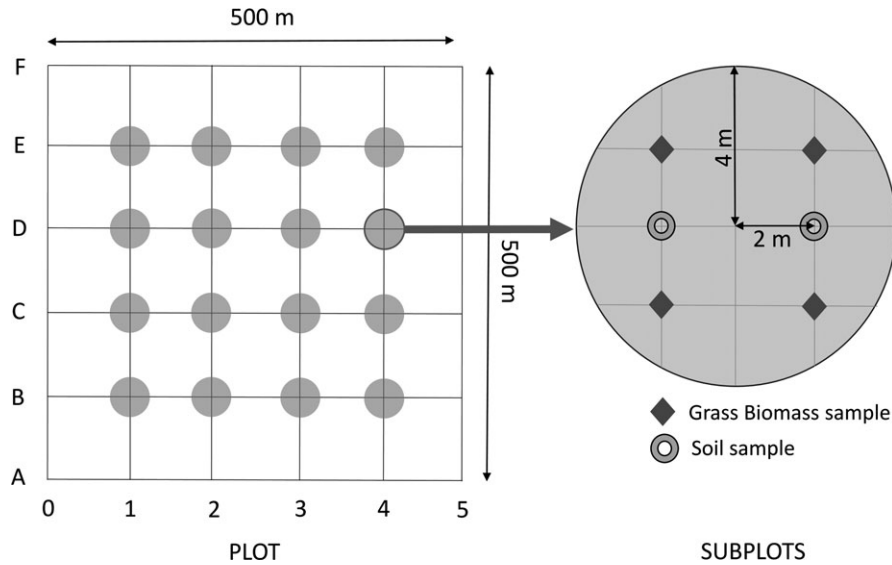


FIGURE 2. Sampling method. Plots were 500 × 500 m (25 ha), with subplots placed every 100 m. Each subplot had a radius of 4 m in which grass and soil (transects 2 and 4 only) measurements were taken.

nomenclature, the Sita and Moutsambote (1988) flora inventory and the Plant list data base (The Plant List, 2013) were used. Species were further categorized into the different life forms (trees, shrubs, sedges, forbs, and grasses). To further categorize shrubs and trees as geoxyllic suffrutex, we used the definition of White (1977) as plants with a ‘massive, woody, underground axes but only annual or short-lived shoots aboveground’, and use the list provided in (Maurin *et al.* 2014). Species diversity was calculated using species richness for all presence/absence data, as the total number of unique species observed in each subplot.

DATA ANALYSIS.—We investigated the within-plot variances using linear models and one-way analysis of variance (ANOVA). To evaluate to what extent species were well sampled, we constructed rarefied species accumulation curves. Dissimilarity in species composition between sites (beta diversity) was calculated using Sørensen dissimilarity index. Compositional patterns were visualized using a non-metric multidimensional scaling (NMDS), and correlations between the floristic composition and environmental characteristics were assessed with multiple regression, by fitting the ecological variables to ordination scores using the ‘envfit’ function of the vegan package (Oksanen *et al.* 2013).

All data analyses were performed using the R statistical software v. 3.1.3 (R Core Team, 2015, <http://cran.r-project.org>), using the vegan (Oksanen *et al.* 2013), spatstat (Baddeley & Turner 2005), pgrmss (Giraudoux 2017), and iNEXT (Hsieh *et al.* 2016) packages.

RESULTS

BIOMASS STOCKS.—In total, we inventoried 4120 live tree stems with a dbh ≥ 10 cm in our 100 hectares field plots (LWR1 = 726, LWR2 = 1480, LLR1 = 1022, and LLR2 = 892),

with a maximum dbh of 39.3 cm. The tree, grass, and saplings/shrubs carbon stocks on a plot basis are summarized in Table 1, with a mean total of 6.47 ± 0.33 MgC/ha. Grass carbon stocks were in general about equal to that of tree, shrub, and sapling biomass combined, though there was considerable variation both within and between plots. Plots had significantly different above-ground biomass for trees (ANOVA single factor, $P < 0.05$) and grasses ($P < 0.01$).

Approximately 90% of the tree AGB was stored in trees with a dbh between 10 and 22 cm, with large stems rare (Supplementary Information Fig. S1). The stem density of the plots varied from 29.0 (plot LWR1) to 59.2 tree stems per hectare (plot LWR2) (Fig. S2).

SOIL CARBON AND NITROGEN.—The mean bulk density of the 0–20 cm horizon was 1.48 ± 0.01 Mg/m³ (LWR2) and 1.44 ± 0.01 Mg/m³ (LLR1) (soil analysis results summarized in Table S1). Carbon stocks and the C:N ratio were very low in both sites. Soil carbon content estimations were very similar in both profiles, being slightly higher in the h0 profile than in the h1, with an average of 16.74 MgC/ha. Carbon stocks and C:N ratios were not significantly different between sites (ANOVA single factor, $P > 0.05$).

We also found that dbh was a predictor of tree height, although with a weak positive relation ($R^2 = 0.14$, $P < 0.001$) in all plots (see Fig. S3 for graph and equation). Ninety percent of the inventoried trees with a dbh ≥ 10 cm were taller than 3.1 m.

SPECIES CHARACTERIZATION.—We identified 49 species in total (4 trees, 13 shrubs, 4 sedges, 17 forbs, and 11 grass species). A complete list of the species is given in the Supplementary Information (Table S2). For trees, *Hymenocardia acida* Tul. (Phyllanthaceae) was hyperdominant, comprising 93.8% of the

TABLE 1. Summary of the average carbon stocks per hectare (MgC/ha). For grasses and saplings/shrubs, \pm indicates the standard error per plot of $16 \times 50.3 \text{ m}^2$ subplots; and for tree stems, it is the standard error of $25 \times 1 \text{ ha}$ subplots.

	Biomass stock (MgC/ha)				Mean
	LWR1	LWR2	LLR1	LLR2	
Grasses					
Stems	0.67 ± 0.11	2.26 ± 0.09	1.39 ± 0.07	0.58 ± 0.04	1.22 ± 0.09
Roots	1.69 ± 0.27	5.65 ± 0.23	3.47 ± 0.16	1.45 ± 0.09	3.06 ± 0.23
Grasses Total	2.34 ± 0.29	7.91 ± 0.25	4.86 ± 0.18	2.03 ± 0.10	4.28 ± 0.25
Saplings/Shrubs					
Stems	0.52 ± 0.13	0.66 ± 0.34	0.64 ± 0.28	0.26 ± 0.10	0.52 ± 0.12
Roots	0.86 ± 0.44	0.57 ± 0.52	0.71 ± 0.70	0.53 ± 0.28	0.63 ± 0.13
Saplings Total	1.38 ± 0.24	1.23 ± 0.42	1.36 ± 0.43	0.79 ± 0.30	1.15 ± 0.18
Trees					
Stems	0.42 ± 0.09	1.01 ± 0.11	0.77 ± 0.16	0.68 ± 0.07	0.74 ± 0.06
Roots	0.18 ± 0.04	0.42 ± 0.05	0.32 ± 0.07	0.24 ± 0.03	0.29 ± 0.02
Trees Total	0.60 ± 0.10	1.42 ± 0.12	1.10 ± 0.17	0.92 ± 0.07	1.03 ± 0.07
Total	4.33 ± 0.41	10.57 ± 0.52	7.31 ± 0.51	3.74 ± 0.32	6.47 ± 0.33

inventoried stems across all plots (Table S3 in Supplementary Information). There were 27 species common to both sites, 3 unique to Lefini, and 11 unique to Lesio Louna. The Sørensen index of dissimilarity between the two sites was 0.21, which indicates a 21% dissimilar species composition between sites. The most abundant grass species in all subplots was *Loudetia simplex* and *Hyparrhenia diplandra*. Poaceae was the dominant family across the plots, followed by Fabaceae and Cyperaceae. Fig. 3A summarizes the number of species per plot divided into vegetation types. Species richness was similar for all plots (LWR1 22, LWR2 25, LLR1 29, and LLR2 23), with a mean of 25 ± 3 . There is a high presence of woody species with a geoxyllic suffrutex growth form (Table S2), and the understory is more diverse.

The rarefied species accumulation curves (Fig. 3B) are comparable among the plots. The estimated sample completeness was for plot LWR1 96%, LWR2 99%, LLR1 93%, and LLR2 97%. When comparing diversity at the subplot level, NMDS ordination showed dissimilarity of the two sites in relation with the species composition of the subplots, but little difference between the two plots within each site (Fig. 4). Variation in species composition is best explained by the distance to forest, elevation, and tree and grass aboveground biomass (NMDS, $P < 0.05$).

DISCUSSION

CARBON STOCKS AND COMPARISON WITH OTHER STUDIES.—At our two sites, the average total vegetation carbon stocks (aboveground and belowground) was 6.5 MgC/ha, with the topsoil horizon (0–20 cm) holding over twice as much, 16.8 MgC/ha (Fig. 5, and considerably more carbon likely stored at deeper depths not investigated here).

The climate of the Bateke Plateau, with annual rainfall of ~1600 mm and an intense 3–4-month dry season, would suggest a closed canopy forest in the absence of disturbances (Sankaran

et al. 2005). Tree cover generally increases with rainfall, but fire is an important disturbance in areas with intermediate precipitation (Staver *et al.* 2011). On Kalahari sands, there is also a gradient of increasing woody cover and biomass with increasing precipitation, at least in the southern section (Scholes *et al.* 2002). Consequently, although we would expect the Bateke to have a high woody cover and tree density, the observed low biomass could be the product of frequent fires, which reduce woody cover and maintain the grasslands (Favier *et al.* 2004, Staver *et al.* 2011), and the sandy soils, which are poor in organic matter and nutrients (Yoka *et al.* 2010) and have a high percolation rate. The high precipitation favors grass productivity, providing more fuel for fires. Savannas with sandy nutrient-poor soils are more likely to favor woody over herbaceous cover (Scholes 1990, Sankaran *et al.* 2005, Bond 2008), although the edaphic conditions can also be a restriction for trees (Mills *et al.* 2013). Tree seedlings compete with grasses for water and nutrients belowground (Scholes & Archer 1997), but disturbances are the main determinants for trees not attaining the maximum woody cover established by water availability (Mills *et al.* 2013).

Although these carbon stock values appear low for savannas, they are not unusual for the Bateke (Table 2). The tree biomass estimated in this study is between the values obtained by Apani (1990) for the Teke Plateau and by Gigaud (2012) for the DRC. Grass biomass is also similar to that calculated by Yoka *et al.* (2013) for the South of RoC and to Makany (1973), but is lower than some other studies (Apani 1990, Yoka *et al.* 2010). This could be due to the timing of the sample collection, which were later in the year than the likely time of maximal grass biomass, around May at the end of the main wet season (Apani 1990, Yoka *et al.* 2010). In the Kalahari sands, Scholes *et al.* (2002) found that grass biomass increased with higher precipitation up to 600 mm and then decreased due to competition with trees (up to 1000 mm). This does not appear to be the case in our two

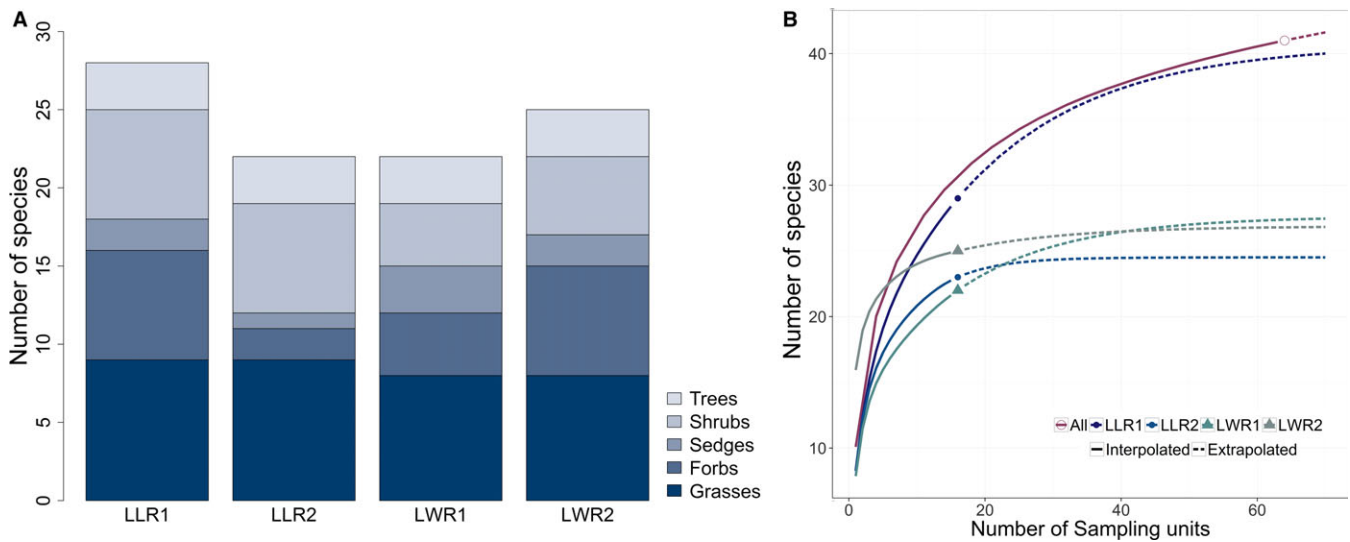


FIGURE 3. (A) Number of species per plot by type (trees, shrubs, sedges, forbs, or grasses) and total. (B) Rarefied species richness showing the cumulative number of species observed and an extrapolated sampling curve (dashed line) of subplot species for all plots ($N = 16$ subplots per plot) and for all combined ($N = 64$).

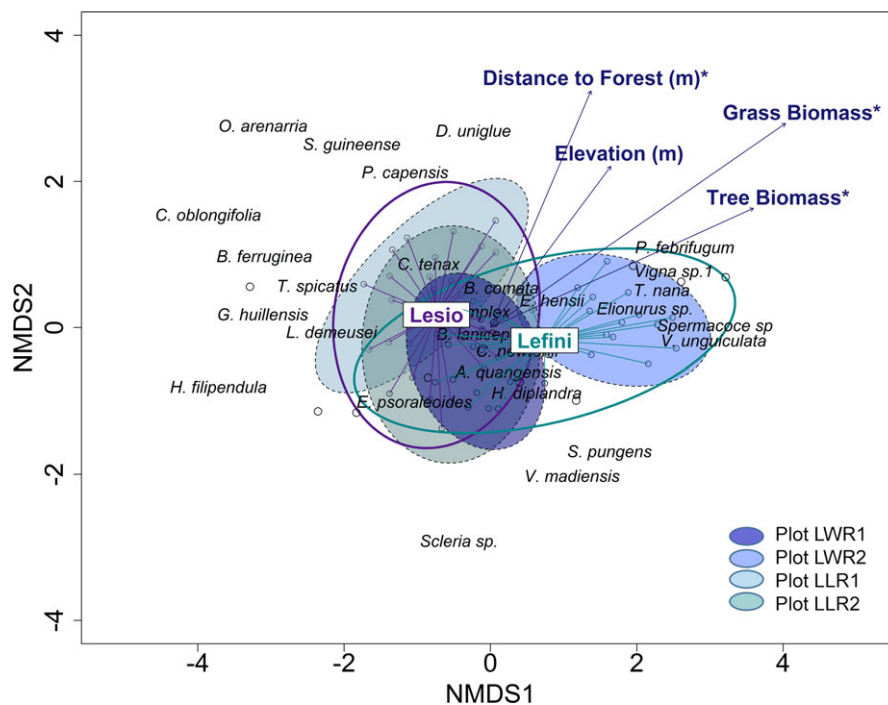


FIGURE 4. Non-metric multidimensional scaling (NMDS) ordination for all the floristic data (grass and woody plants). Big circles grouping the sites (Lesio Louna [LLR] and Lefini [LWR]), fill circles grouping the subplots (LWR1, LWR 2, LLR1, and LLR2), with confidence limit for ellipses of 0.95. Floristic composition was correlated with environmental vectors, displayed as arrows (where $P < 0.05$, and * where $P < 0.01$). Elevation (m) = elevation relative to lowest point in each plot.

sites, but further research about tree–grass competition is needed to better understand this system.

The biomass of saplings/shrubs was higher than might be expected from a visual assessment, which suggests a landscape dominated by grass and scattered trees. The density of shrubs in

this landscape was very patchy, and the subplot density measurements have a non-normal, right-skewed distribution, with many plots not having any shrubs, and some containing high densities. Larger or more subplots would be required for a more robust shrub biomass estimation.

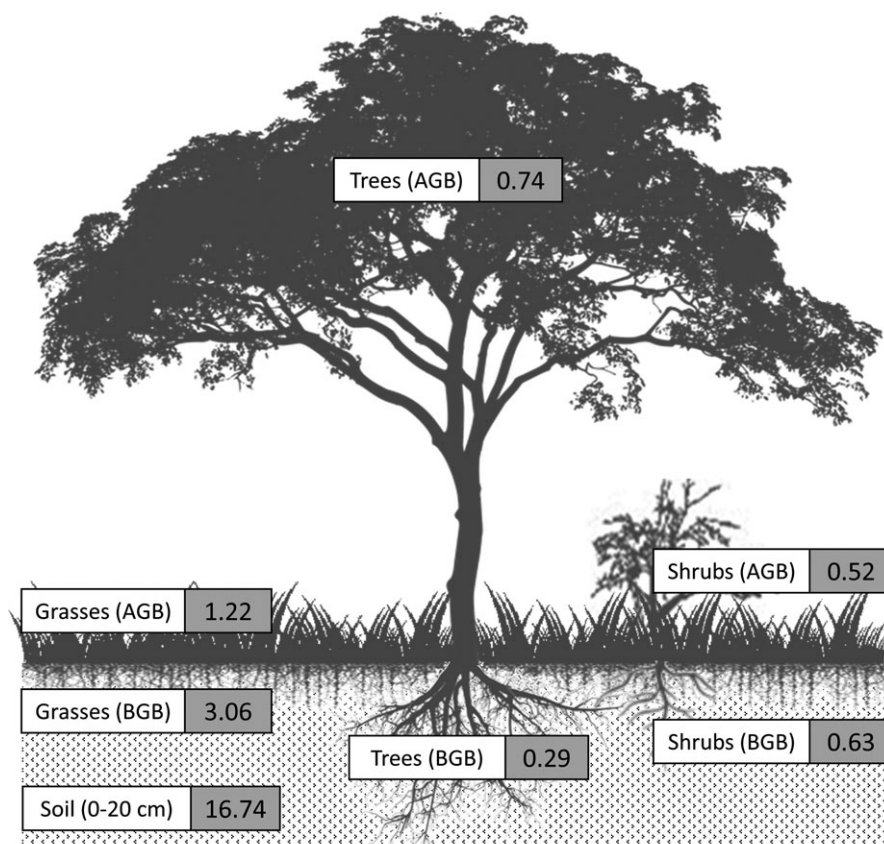


FIGURE 5. Representation of the average carbon stocks (MgC per hectare) for all the plots in the study sites. Soil is Soil Organic Carbon (SOC) stock.

Few studies have quantified the BGB in the Bateke, but our results are similar to those obtained by Apani (1990) for grasses and Lokegna (2015) for trees. These values (mean \pm) are low compared to reported general tropical savannas root biomass, such as the 6.48 MgC/ha reported by Jackson *et al.* (1996) for tropical grassland savannas. Tree, shrub, and grass BGB were estimated with ratios found in the literature, and therefore, having local allometric equations would provide better estimates. Moreover, we might have underestimated by using the mean root-to-shoot ratio described by Ryan *et al.* (2011), as this ratio varied from 0.27 to 0.58. The BGB of the geoxyllic suffrutex species will have been underestimated as they contain disproportionately large underground structures.

Our savanna plots were characterized by a very low tree stem density (averaging 41.2 stems per ha) and low biomass, consistent with systems with high disturbance. This result indicates the importance of using large (>10 ha) plot areas for the inventory of this biome, as savannas are highly heterogeneous. However, in order to capture all landscape variability, larger scales of sampling would be needed (Staver 2017).

The topsoil contributes the most to the carbon pool in our plots (16.7 MgC/ha, 53% of the total), in concordance with other studies of savannas (Scurlock & Hall 1998, Ciais *et al.* 2011), and the low carbon density of these soils is similar to other studies in Kalahari sands (Bird *et al.* 2004). Soil carbon stocks are similar to

those found in other studies of the Bateke Plateau (Table 2), such as Ifo (2017), and slightly lower than Schwartz and Namri (2002). Additionally, these values are much lower than in miombo woodlands, where the median soil C stocks (0–30 cm) were 35.9 tC/ha, but supporting a much higher aboveground woody biomass of 28.7 tC/ha (Ryan *et al.* 2016). Carbon content estimations were very similar in both profiles, being slightly higher in the h0 profile than in h1. These carbon stock estimations are important for further studies, to inform conservation measures and in the design of more effective data collection protocols.

SPECIES DIVERSITY AND COMMUNITY COMPOSITION.—The floristic inventory results are in concordance with those of other authors for the Bateke (Duvigneaud (1953a), Makany (1973) and Nsongola *et al.* (2006)). Most of the tree species inventoried are typical of dry savannas (Duvigneaud 1949). Many authors in fact denominate this type of savanna of the Bateke as *Hymenocardia* savanna (Duvigneaud 1953a, Descoigns 1972, Makany 1973), dominated by *Hyparrhenia diplandra* or by *L. simplex* (e.g., Makany 1973, Walters *et al.* 2013). *H. acida*, is a deciduous, fire-tolerant (Trapnell 1959), small tree that occurs in tropical African savannas mainly on sandy, loamy, or clayey soils (Duvigneaud 1949). It reproduces asexually through production of resprouts, stimulated by frequent fires (Walters 2012). Koechlin (1960) described that he never saw a *H. acida* seedling in the area, which implies the

TABLE 2. Allocation of carbon stocks (MgC/ha) in the Bateke Plateau savannas from different studies.

	Grasses (MgC/ha)		Trees (MgC/ha)		Soil (MgC/ha)	Area
	Roots	Stems	Roots	Stems		
Makany (1973)		1.39 ⁽¹⁾ –1.71 ⁽²⁾				Plateaux Teke RoC
Apani (1990)	4.31	1.78		0.17 ^a		Plateaux Teke RoC
Gigaud (2012)				1.66 ^a		Bateke DRC
Lokegna (2015)			1.85 ^a			Bateke (Mah) RoC
Yoka <i>et al.</i> (2010)		1.72 ⁽¹⁾ –4.79 ⁽²⁾				Cuvette RoC
Yoka <i>et al.</i> (2013)		1.18 ⁽¹⁾ –2.63 ⁽²⁾				Cuvette RoC
Schwartz and Namri (2002)					15–20 (0–10 cm)	Bateke RoC
					86–102 (0–100 cm) ^b	
Ifo (2017)					13.28 (0–20 cm)	Lesio Louna RoC
					45.95 (0–100 cm)	
<i>This study</i>	3.06 ± 0.23	1.22 ± 0.09	0.29 ± 0.02	0.74 ± 0.06	16.74 ± 0.9 (0–20 cm)	Lefini/Lesio Louna RoC

Notes: ⁽¹⁾*Loudetia simplex*; ⁽²⁾*Hyparbenia diplandra*.

^aTrees and shrubs.

^bAverage of the Bateke land unit.

importance of vegetative reproduction (Walters 2007). Boaler and Sciwale (1966) found for miombo woodlands that *H. acida* was one of the fastest growing trees, therefore potentially making them grow quickly enough to escape mortality by fire in places given enough precipitation, like in the Bateke. These characteristics of *H. acida* could explain its hyperdominance in this system.

In our inventory, we found six shrubs and trees with a geoxyllic suffrutex growth form (Table S1), indicating a pyrophytic component of the flora and potentially an established savanna in a climate suitable for forests (White 1977, Walters *et al.* 2006, Maurin *et al.* 2014). We have also found some Cyperaceae species, which often occupy recently burned grasslands, and some pyrophytes, including *H. acida*, *A. senegalensis*, *Bridelia ferruginea*, *Psorospermum febrifugum*, and *Maprounea africana* (Walters *et al.* 2006), which highlights the importance of fire in maintaining these ecosystems. Fire is likely responsible for maintaining the forest–savanna mosaic with abrupt boundaries between forest and savanna areas. We did not find savanna–forest transition species found in similar habitats, like Walters *et al.* (2006) in Gabon, perhaps indicating the savanna at our sites has been stable for some time.

The species diversity we found is quite low compared to other African savannas, for example in South Africa (Fynn *et al.* 2004, Smith *et al.* 2016) and for miombo woodlands (Masocha *et al.* 2011). The species richness is more comparable to values obtained for natural grasslands in South Africa, and greater than those for any secondary grasslands (Zaloumis & Bond 2016), suggesting these savannas are not new and probably have existed as a mosaic for long time. We also did not find any endemic species in our inventory, with most of them having wider distributions in Africa. However, we only subsampled 100 ha of savanna, from two sites located only 86 km apart, so our conclusions about plant diversity cannot be assumed to apply to the whole plateau. In Gabon, Wieringa and Sosef (2011) found for

the Batéké Plateau National Park a relatively unique flora with a limited spatial extent, and Walters *et al.* (2006) encountered more endemism in forests than in savannas. Although the Bateke belongs to the Guineo-Congolian regional center of endemism (White 1983), some studies had found species distributions similar to other regions. Walters *et al.* (2006) concluded in their analysis about floristics in the Gabon's Bateke Plateau that over 50 percent of the species were classified as Guineo-Congolian, but 20 percent had extended distributions into the Zambezi or Sudanian phytochoria, and that sites on Kalahari sands in Gabon shared floristic affinities with Lefini. Similarly, Koechlin (1960) determined for the Kalahari sand savannas in the south of RoC that 12% of the species were endemic and 55% had a Sudano-Angolan distribution (Walters *et al.* 2006). Duvigneaud (1953a) described the Kalahari plateau in the DRC (Kwango) as an intermediate zone, with a Guineo-Congolaise climate but with Zambezi elements due to the edaphic conditions. Additionally, Fayolle *et al.* (2018) concluded, using the data presented here, that Lefini and Lesio Louna have floristic similarities with Northern and Western African savannas and woodlands. The mixed floristic composition of the Bateke is likely due to its historical spatial geography. These savannas have been fairly isolated from other savanna formations, with only some exceptions. The floristic affinities with the south and east could be explained by a connection via a savanna corridor with the Angolan highlands (Fayolle *et al.* 2018) and by the Kalahari sands sheets, which could have provided a connection with southern species, although this hypothesis remains uncertain (Walters *et al.* 2006). The similarities with the northern savannas could be explained by the fragmentation of the Congo Basin forest during the Last Glacial Maximum (18000 years ago) (Maley 1991, Fayolle *et al.* 2018). Furthermore, the Sangha River Interval provided a large savanna corridor connecting the Sudanian savannas in the north to the Bateke savannas (Maley 2001, Maley & Willis 2010, Bostoen *et al.* 2015).

CONCLUSION

Our results show that the Bateke savannas store only small quantities of carbon per hectare, with the largest pools in the soil and roots. Its species diversity is low, and we found no evidence of endemism. The savanna ecosystem is clearly controlled by fire, with all plants showing adaption to regular burning. We have further shown the need to use large plots (>10 ha) to capture variations in carbon stocks and species diversity in this area. These data will thus inform future studies on optimal sampling methodologies and carbon dynamics in this ecosystem. Our results, although only representative of part of the Bateke, will further help in understanding the complex relationship between grasses, understory plants, trees, fire, and resources. However, more studies are needed in this ecosystem to inform conservation and restoration, particularly with regard to fire regime, and to understand future challenges from climate change.

ACKNOWLEDGMENTS

Funding for this work was provided by the US Forest Service (USFS) and the University of Edinburgh. We thank USFS and Wildlife Conservation Society-Congo (WCS) for providing logistics and institutional support. We thank numerous field assistants (Roland Odende, Marcelle Armande Batsa Mouwembe, Ledia Bidounga, and Onesi Samba) and ecoguards of Lefini and Ibou Briko, Prime Mobie and Denis Ngatse, for their invaluable help and knowledge; Mr. Gilbert Nsongola for helping with the species identification; and the people of Mpoh and Mâh for maintaining the firebreaks and for sharing their knowledge about fire use. Edward T. A. Mitchard and Casey M. Ryan were supported by the NERC-funded Socio-Ecological Observatory for the Southern African Woodlands (NE/P008755/1).

DATA AVAILABILITY

Data used in this study are archived at the Dryad Digital Repository: doi.org/10.5061/dryad.2122768 (Nieto-Quintano *et al.* 2018). Information on using the vegetation data prior to the end of the embargo can be found at seosaw.github.io.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

TABLE S1. *Soil characteristics of Lefini and Lesio Louna.*

TABLE S2. *Species composition list (presence/absence data) for all subplots.*

TABLE S3. *Stem species number per plot for all trees.*

FIGURE S1. AGB and cumulative sum of AGB vs. dbh classes for all plots for trees.

FIGURE S2. Density of stems per hectare for all plots, with box and whisker data based on individual values for the 25 × 1 ha subplots within each 25 ha plot.

FIGURE S3. Dbh vs Height for all trees in all plots, with point density.

LITERATURE CITED

- APANI, E. 1990. Contribution à l'étude phytoécologique de la savane a Loude-tia demeusei et Hymenocardia acida des contreforts des Plateaux Téké (République Populaire du Congo). PhD Dissertation. Université de Rennes.
- AUBREVILLE, A. 1949. Climats, forêts et désertification de l'Afrique tropicale. Société d'éditions géographiques, maritimes et coloniales, Paris. p. 351.
- AUBREVILLE, A. 1961. Flore du Gabon. France, Paris.
- AUBREVILLE, A. 1962. Savanisation tropicale et glaciations quaternaires. *Adan-sonia* 2: 16–84.
- BADDELEY, A., AND R. TURNER. 2005. spatstat: An R Package for Analyzing Spatial Point Patterns. *J. Stat. Softw.* 12: 1–42.
- BAMPS, P. 2013. A new species of Kalaharia (Lamiaceae) from Central Africa. *Plant Ecology and Evolution* 146: 134–137.
- BATSA, M. A., S. A. IFO, S. BINSANGOU, AND F. KOUBOUANA. 2017. Variabilité spatiale des stocks de carbone organique du sol des savanes dans les réserves de Lésio-Louna et de Lefini, plateaux Tékés, République du Congo. *Afrique SCIENCE* 13: 297–307.
- BIRD, M. I., E. M. VEENENDAAL, AND J. J. LLOYD. 2004. Soil carbon inventories and $\delta^{13}C$ along a moisture gradient in Botswana. *Glob. Change Biol.* 10: 342–349.
- BLAKE, G. R., AND K. H. HARTGE. 1986. Bulk density. Soil Science Society of America, Madison, WI.
- BOALER, S. B., AND K. C. SCIWALE. 1966. Ecology of a Miombo Site, Lupa North Forest Reserve, Tanzania: III. effects on the vegetation of local cultivation practices. *J. Ecol.* 54: 577–587.
- BOND, W. J. 2008. What limits trees in C4 grasslands and savannas? *Annu. Rev. Ecol. Evol. Syst.*, 39: 641–659.
- BOND, W., AND N. P. ZALOUIS. 2016. The deforestation story: Testing for anthropogenic origins of Africa's flammable grassy biomes. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 371: 20150170.
- BOSTOEN, K., B. CLIST, C. DOUMENGE, R. GROLLEMUND, J. M. HOMBERT, J. K. MULUWA, AND J. MALEY. 2015. Middle to late holocene paleoclimatic change and the early bantu expansion in the rain forests of Western Central Africa. *Current Anthropology* 56: 354–384.
- BRANSBY, D. I., AND N. M. TAINTON. 1977. The disc pasture meter: Possible applications in grazing management. *Proceedings of the Annual Con-gresses of the Grassland Society of Southern Africa* 12: 115–118.
- CHAMPLUVIER, D., AND F. DOWSETT-LEMAIRE. 1999. Vascular plants from Odzala National Park: Commented list of species new for Congo-Brazzaville. *Syst. Geogr. Plants* 69: 9–28.
- CHAVE, J., D. COOMES, S. JANSEN, S. L. LEWIS, N. G. SWENSON, AND A. E. ZANNE. 2009. Towards a worldwide wood economics spectrum. *Ecol. Lett.* 12: 351–366.
- CHAVE, J., M. RÉJOU-MÉCHAIN, A. BÚRQUEZ, E. CHIDUMAYO, M. S. COLGAN, W. B. C. DELITTI, A. DUQUE, D. WELINGTON, P. M. FEARNSIDE, R. GOODMAN, M. HENRY, A. MARTÍNEZ-YRÍZAR, W. MUGASHA, H. MULLER-LANDAU, M. MENCUCINI, B. NELSON, A. NGOMANDA, E. NOGUEIRA, E. ORTIZMALAVASSI, R. PÉLISSIER, P. PLOTON, C. RYAN, AND G. VIEILLE-DENT. 2014. Improved Allometric Models to Estimate the Above-ground Biomass of Tropical Trees. *Global Change Biology* 20(10): 3177–3190. doi:10.1111/gcb.12629.
- CIAIS, P., A. BOMBELLI, M. WILLIAMS, S. L. PIAO, J. CHAVE, C. M. RYAN, M. HENRY, P. BRENDER, AND R. VALENTINI. 2011. The carbon balance of Africa: Synthesis of recent research studies. *Philos Trans A Math Phys Eng Sci* 369: 2038–2057.
- Congo basin forest partnership. 2006. The Forests of the Congo Basin. State of the Forest 2006. *In* Congo basin forest partnership (Ed.) 255 pages.
- DECHAMPS, R., R. LANFRANCHI, A. LE COCQ, AND D. SCHWARTZ. 1988. Recon-stitution d'environnements quaternaires par l'étude de macrorestes

- vegetaux. (Pays Bateke, R.P. du Congo). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 66: 33–44.
- DESCOIGNS, B. 1960. Rapport botanique préliminaire sur la Cuvette congolaise (République du Congo). Rapport d'étude n° 4, p. 15. ORSTOM.
- DESCOIGNS, B. 1972. Notes de phytocologie équatoriale les steppes loussek du plateau Bateke (Congo). *Adansonia* 2: 569–584.
- DÖRGELOH, W. G. 2002. Calibrating a disc pasture meter to estimate above-ground standing biomass in Mixed Bushveld, South Africa. *Afr. J. Ecol.* 40: 100–102.
- DUVIGNEAUD, P. 1949. Les Savanes du Bas-Congo: essai de phytosociologie topographique. Les Presses de "Lejeunia", Liège.
- DUVIGNEAUD, P. 1953a. La Flore et la végétation du Congo Meridional. *Lejeunia* 16: 95–124.
- DUVIGNEAUD, P. 1953b. Les formations herbeuses (savanes et steppes) du Congo meridional. *Les Naturalistes Belges* 34: 66–75.
- ELENGA, H., D. SCHWARTZ, AND A. VINCENS. 1994. Pollen evidence of late Quaternary vegetation and inferred climate changes in Congo. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 109: 345–356.
- FAVIER, C., J. CHAVE, A. FABING, D. SCHWARTZ, AND M. A. DUBOIS. 2004. Modelling forest-savanna mosaic dynamics in man-influenced environments: Effects of fire, climate and soil heterogeneity. *Ecol. Model.* 171: 85–102.
- FAYOLLE, A., M. D. SWAINE, J. ALEMAN, A. F. AZIHO, AND D. BAUMAN. M. te BEEST, E. CHIDUMAYO, J. CROMSIGHT, M. FINCKH, F. MAIATO, P. GONÇALVES, J. GILLET, A. GOREL, A. HICK, R. HOLDO, B. KIRUNDA, G. MAHY, I. McNICOL, C. M. RYAN, R. REVERMANN, A. PLUMPTRE, R. PRITCHARD, P. NIETO-QUINTANO, C. B. SCHMIDT, J. SEGHERI, T. SWEMMER, H. TELILA, AND E. WOOLLEN. 2018. A sharp floristic discontinuity revealed by the biogeographic regionalization of African savannas. Under Review (*Journal of Biogeography*)
- FORESTA, H. 1990. Origine et évolution des savanes intramayombiennes (R.P. du Congo). II. Apports de la botanique forestière. *Paysages quaternaires de l'Afrique centrale atlantique*, pp. 326–335. Orstom, Paris.
- FYNN, R. W. S., C. D. MORRIS, AND T. J. EDWARDS. 2004. Effect of burning and mowing on grass and forb diversity in a long-term grassland experiment. *Appl. Veg. Sci.* 7: 1–10.
- GIGAUD, M. 2012. Etat des jachères forestières du Plateau Batéké et, possibilité de les restaurer par Régénération Naturelle Assistée (RNA) Projet Makala, République Démocratique du Congo. MSc Dissertation. Environnement et Sociétés. Université d'Orléans, Montpellier.
- GIRAUDOUX, P. 2017. *pgirmess: Data analysis in ecology*. R Package Version 1(6): 7.
- HADDON, I. G. 2000. Kalahari group sediments. In T. C. Partridge, and R. R. Maud (Eds.). *The cenozoic of southern Africa*, oxford monographs on geology and geophysics, vol 40, pp. 173–181. Oxford University Press, New York.
- HALL, D. O., AND J. M. O. SCURLOCK. 1991. Climate change and productivity of natural grasslands. *Ann. Bot.* 67: 49–55.
- HARRIS, I., P. D. JONES, T. J. OSBORN, AND D. H. LISTER. 2014. Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset. *Int. J. Climatol.* 34: 623–642.
- HIGGINS, S. I., W. J. BOND, AND W. S. W. TROLLOPE. 2000. Fire, resprouting and variability: A recipe for grass-tree coexistence in savanna. *J. Ecol.* 88: 213–229.
- HOARE, A. L. 2007. The use of non-timber forest products in the Congo Basin: Constraints and Opportunities. In *The Rainforest Foundation* (Ed.). London, United Kingdom. 53 pages.
- HSIEH, T. C., K. H. MA, AND A. CHAO. 2016. iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol. Evol.* 7: 1451–1456.
- IFO, S. A. 2017. Variation of $\delta^{13}C$ and soil organic carbon dynamics in the savannah of Plateau Bateke, Congo Basin. *International Journal of Scientific & Technology Research* 6(01). 181–185.
- IUCN, and UNEP. 2015. World Database on Protected Areas (WDPA). UNEP-WCMC, Cambridge, UK.
- JACKSON, R. B., J. CANADELL, J. R. EHLERINGER, H. A. MOONEY, O. E. SALA, AND E. D. SCHULZE. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* 108: 389–411.
- KOECHLIN, J. 1960. La végétation des savanes du sud de la République du Congo. PhD Dissertation. Faculté des Sciences de Montpellier, Montpellier.
- LACHENAUD, O. 2009. The vascular plant flora of the Republic of Congo: New records. *Syst. Geogr. Plants* 79: 199–214.
- LOKEGNA, D. 2015. Biomasse racinaire des arbustes des savanes des Plateaux Tekes. MSc Dissertation. Ecole Nationale Supérieure d'Agronomie et de Foresterie. Université Marien Ngouabi, Brazzaville.
- van der MAESEN, J., AND G. M. WALTERS. 2011. Novitates Gabonenses 77: A new *Eriosema* (Leguminosae-Papilionoideae) from Gabon and adjacent Congo. *Plant Ecology and Evolution* 144: 101–105.
- MAKANY, L. 1973. Recherches sur la végétation des plateaux Batekes (Congo) PhD Dissertation. Université Pierre et Marie Curie (Paris).
- MALEY, J. 1991. The African rain forest vegetation and palaeoenvironments during late quaternary. *Clim. Change.* 19: 79–98.
- MALEY, J. 2001. La destruction catastrophique des forêts d'Afrique centrale survenue il y a environ 2500 ans exerce encore une influence majeure sur la répartition actuelle des formations végétales. *Syst. Geogr. Plants* 71: 777–796.
- MALEY, J., AND K. WILLIS. 2010. Did a savanna corridor open up across the Central African Forests 2500 years ago? *CoForChange Newsletters* (2). 5 pages.
- MAMPOUYA, E. 2015. Biodiversité et variabilité de la densité du bois des arbustes de savane dans les environs du village Mâh (Plateaux TEKE, République du Congo). MSc Dissertation. Ecole Nationale Supérieure d'Agronomie et de Foresterie. Université Marien Ngouabi, Brazzaville.
- MASOCHA, M., A. K. SKIDMORE, X. POSHIWA, AND H. H. T. PRINS. 2011. Frequent burning promotes invasions of alien plants into a mesic African savanna. *Biol. Invasions* 13: 1641–1648.
- MAURIN, O., T. J. DAVIES, J. E. BURROWS, B. H. DARU, K. YESSOUFOU, A. M. MUASYA, M. van der BANK, AND W. J. BOND. 2014. Savanna fire and the origins of the 'underground forests' of Africa. *New Phytol.* 204: 201–214.
- MENAUT, J. C. 1983. The vegetation of African Savannas. *Tropical Savannas. Ecosystems of the World* 13: 109–149.
- MILLS, A. J., A. V. MILEWSKI, M. V. FEY, A. GRÖNGRÖFT, A. PETERSEN, AND C. SIRAMI. 2013. Constraint on woody cover in relation to nutrient content of soils in western southern Africa. *Oikos* 122: 136–148.
- NAMRI, M. 1996. Les stocks de carbone des sols du Congo: bilan spatial et recherche des facteurs de répartition. MSc Dissertation. UFR de Géographie. Université Louis Pasteur, Strasbourg.
- NIETO-QUINTANO, P., E. T. A. MITCHARD, R. ODEDE, M. A. BATSA MOWEMBE, T. RAYDEN, AND C. M. RYAN. 2018. Data from: The mesic savannas of the Bateke Plateau: carbon stocks and floristic composition. Dryad Digital Repository. <https://doi.org/10.5061/dryad.2122768>.
- NSONGOLA, G., L. OKANDZA, J. OMBANI, AND T. KING. 2006. Liste illustrée des plantes des Réserves Lesio-Louna et Lefini, édition 1.1. In *John Aspinall Foundation/CERVE* (Ed.). Report. Brazzaville, Congo. 48 pages.
- ODEDE, R. 2016. Etude comparative de la flore des savanes des réserves de la Lefini et de la Lesio-Louna dans les Plateaux Tékés. MSc Dissertation. Université Marien Ngouabi.
- OKSANEN, J., F. G. BLANCHET, R. KINDT, P. LEGENDRE, P. R. MINCHIN, R. B. O'HARA, G. L. SIMPSON, P. SOLYMOS, M. H. H. STEVENS, AND H. WAGNER. 2013. *vegan: Community Ecology Package*, R package version 2.0-10.
- OLSON, D. M., E. DINERSTEIN, E. D. WIKRAMANAYAKE, N. D. BURGESS, G. V. N. POWELL, E. C. UNDERWOOD, J. A. D'AMICO, I. ITUA, H. E. STRAND, J. C. MORRISON, C. J. LOUCKS, T. F. ALLNUTT, T. H. RICKETTS, Y. KURA, J. F. LAMOREUX, W. W. WETTENGEL, P. HEDAO, AND K. R. KASSEM. 2001. Terrestrial ecoregions of the world: A new map of life on Earth. *Bioscience* 51: 933–938.

- OSLISLY, R., L. WHITE, I. BENTALEB, C. FAVIER, M. FONTUGNE, J. F. GILLET, AND D. SEBAG. 2013. Climatic and cultural changes in the west Congo Basin forests over the past 5000 years. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 368: 20120304.
- R Core Team. 2015. R Foundation for Statistical Computing. R: A Language and Environment for Statistical Computing, Vienna, Austria.
- RAYDEN, T., N. MABIALA, A. TSOMOU, AND L. ESCOUFLAIRE. 2014. Batéké Lefini Landscape Project Annual report. *In* W. C. S. Carpe (Ed.). V2. 27 pages.
- REVERMANN, R., F. M. GONÇALVES, A. L. GOMES, AND M. FINCKH. 2017. Woody species of the miombo woodlands and geoxylic grasslands of the cusseque area, south-central Angola. Check List, The Journal of Biodiversity Data, 13(1) Article 2030. 1–10.
- ROBYNS, W. 1949. Flore du Congo Belge et du Ruanda-Urundi. Bulletin du Jardin botanique de l'État à Bruxelles 19.
- RYAN, C. M. 2009. Carbon Cycling, Fire and Phenology in a Tropical Savanna Woodland in Nhambita, Mozambique. PhD Dissertation. University of Edinburgh.
- RYAN, C. M., R. PRITCHARD, I. McNICOL, M. OWEN, J. A. FISHER, AND C. LEHMANN. 2016. Ecosystem services from southern African woodlands and their future under global change. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 371: 20150312.
- RYAN, C. M., M. WILLIAMS, AND J. GRACE. 2011. Above- and belowground carbon stocks in a miombo woodland landscape of mozambique. *Biotropica* 43: 423–432.
- SANKARAN, M., N. P. HANAN, R. J. SCHOLES, J. RATNAM, D. J. AUGUSTINE, B. S. CADE, J. GIGNOUX, S. I. HIGGINS, X. Le ROUX, F. LUDWIG, J. ARDO, F. BANYIKWA, A. BRONN, G. BUCINI, K. K. CAYLOR, M. B. COUGHENOUR, A. DIOUF, W. EKAYA, C. J. FERAL, E. C. FEBRUARY, P. G. H. FROST, P. HIERNAX, H. HRABAR, K. L. METZGER, H. H. T. PRINS, S. RINGROSE, W. SEA, J. TEWS, J. WORDEN, AND N. ZAMBATIS. 2005. Determinants of woody cover in African savannas. *Nature* 438: 846–849.
- SCHOLES, R. J. 1990. The influence of soil fertility on the ecology of southern African dry savannas. *J. Biogeogr.* 17: 415–419.
- SCHOLES, R. J., AND S. R. ARCHER. 1997. Tree-grass interactions in Savannas. *Annu. Rev. Ecol. Evol. Syst.* 28: 517–544.
- SCHOLES, R. J., P. R. DOWTY, K. CAYLOR, D. A. B. PARSONS, P. G. H. FROST, AND H. H. SHUGART. 2002. Trends in savanna structure and composition along an aridity gradient in the Kalahari. *J. Veg. Sci.* 13: 419–428.
- SCHWARTZ, D. 1988. Some podzols on Bateke sands and their origins, People's Republic of Congo. *Geoderma* 43: 229–247.
- SCHWARTZ, D. 1992. Climatic drying about 3000 BP and Bantu expansion in Atlantic Central Africa: Some reflections. *Bulletin - Societe Geologique de France* 163: 353–361.
- SCHWARTZ, D., R. DECHAMPS, H. ELENGA, R. LANFRANCHI, A. MARIOTTI, AND A. VINCENS. 1995. Les savanes du Congo: Une végétation spécifique de l'holocène supérieur. 2e Symposium de Palynologie africaine, Tervuren (Belgique) Publ. Occas. CIFEG, 1995/31, Orléans, CIFEG, 99–108.
- SCHWARTZ, D., AND M. NAMRI. 2002. Mapping the total organic carbon in the soils of the Congo. *Glob Planet Change* 33: 77–93.
- SCURLOCK, J. M. O., AND D. O. HALL. 1998. The global carbon sink: A grassland perspective. *Glob. Change Biol.* 4: 229–233.
- SITA, P., AND J. M. MOUTSAMBO. 1988. Catalogue des plantes vasculaires du Congo. ORSTOM, Centre d'Etudes sur les Ressources Vegetales, Brazzaville, Congo.
- SMITH, M. D., A. K. KNAPP, S. L. COLLINS, D. E. BURKEPILE, K. P. KIRKMAN, S. E. KOERNER, D. I. THOMPSON, J. M. BLAIR, C. E. BURNS, S. EBY, E. J. FORRESTEL, R. W. S. FLYNN, N. GOVENDER, N. HAGENAH, D. L. HOOVER, AND K. R. WILCOX. 2016. Shared drivers but divergent ecological responses: Insights from long-term experiments in Mesic Savanna Grasslands. *Bioscience* 66: 666–682.
- SMITH, M. D., B. W. VAN WILGEN, C. E. BURNS, N. GOVENDER, A. L. F. POTGIETER, S. ANDELMAN, H. C. BIGGS, J. BOTHA, AND W. S. W. TROLLOPE. 2013. Long-term effects of fire frequency and season on herbaceous vegetation in savannas of the Kruger National Park, South Africa. *J. Plant Ecol.* 6: 71–83.
- SOSEF, M. S. M. E. A. 2006. The Checklist of Gabonese Vascular Plants.
- SOSEF, M. S. M., G. DAUBY, A. BLACH-OVERGAARD, X. VAN DER BURGT, L. CATARINO, T. DAMEN, V. DEBLAUWE, S. DESSEIN, J. DRANSFIELD, V. DROISSART, M. C. DUARTE, H. ENGLEDDOW, G. FADEUR, R. FIGUEIRA, R. E. GEREAU, O. J. HARDY, D. J. HARRIS, J. DE HEIJ, S. JANSSENS, Y. KLOMBERG, A. C. LEY, B. A. MACKINDER, P. MEERTS, J. L. VAN DE POEL, B. SONKÉ, T. STÉVART, P. STOFFELEN, J. C. SVENNING, P. SEPULCHRE, R. ZAISS, J. J. WIERINGA, AND T. L. P. COUVREUR. 2017. Exploring the floristic diversity of tropical Africa. *BMC Biol.* 15:15. 1–23.
- STAYER, A. C. 2018. Prediction and scale in savanna ecosystems. *New Phytol.* 219: 52–57.
- STAYER, A. C., S. ARCHIBALD, AND S. A. LEVIN. 2011. The global extent and determinants of savanna and forest as alternative biome states. *Science* 334: 230–232.
- The Plant List. 2013. Version 1. Available at: <http://www.theplantlist.org/> (accessed August 2017).
- TRAPNELL, C. G. 1959. Ecological results of woodland and burning experiments in northern Rhodesia. *J. Ecol.* 47: 129–168.
- VELDMAN, J. W., L. A. BRUDVIG, E. I. DAMSCHEN, J. L. ORROCK, W. B. MATTINGLY, AND J. L. WALKER. 2014. Fire frequency, agricultural history and the multivariate control of pine savanna understorey plant diversity. *J. Veg. Sci.* 25: 1438–1449.
- VELDMAN, J. W., E. BUISSON, G. DURIGAN, G. W. FERNANDES, S. Le STRADIC, G. MAHY, D. NEGREIROS, G. E. OVERBECK, R. G. VELDMAN, N. P. ZALOUIS, F. E. PUTZ, AND W. J. BOND. 2015. Toward an old-growth concept for grasslands, savannas, and woodlands. *Front. Ecol. Environ.* 13: 154–162.
- VINCENS, A., D. SCHWARTZ, H. ELENGA, I. REYNAUD-FARRERA, A. ALEXANDRE, J. BERTAUX, A. MARIOTTI, L. MARTIN, J. D. MEUNIER, F. NGUETSOR, M. SERVANT, S. SERVANT-VILDARY, AND D. WIRRMANN. 1999. Forest response to climate changes in Atlantic Equatorial Africa during the last 4000 years BP and inheritance on the modern landscapes. *J. Biogeogr.* 26: 879–885.
- WALTERS, G. 2007. Fire Primer for the Batéké Plateaux, Central Africa. *In* Missouri Botanical Garden, USA. Internal report to the Rufford Foundation. 42 pp.
- WALTERS, G. 2010a. The Land Chief's embers: ethnobotany of Batéké fire regimes, savanna vegetation and resource use in Gabon. PhD Dissertation. University College London.
- WALTERS, G. 2010b. Savanna burning yesterday and today in Gabon's Bateke Plateaux: Foraging-fires and ecosystem effects. *In* UCL (Ed.). 17 pp.
- WALTERS, G. 2012. Customary fire regimes and vegetation structure in Gabon's Bateke Plateaux. *Human Ecology* 40: 943–955.
- WALTERS, G., A. BRADLEY, AND R. NIANGADOUMA. 2006. Floristics of Gabon's Bateke Plateaux: Guineo-Congolian plants on Kalahari Sands. *In* Taxonomy and Ecology of African Plants, their Conservation and Sustainable Use, S. A. Gazanfar, and H. J. Beentje, eds., London: Royal Botanic Gardens Kew, pp. 259–266.
- WALTERS, G., I. PARMENTIER, AND T. STÉVART. 2013. Diversity and conservation value of Gabon's savanna and inselberg open vegetation: An initial gap analysis. *Plant Ecology and Evolution*, 145(1), 46–54.
- WHITE, F. 1977. The underground forests of Africa: A preliminary review. *Gardens' Bulletin, Singapore* 29: 57–71.
- WHITE, F. 1979. The Guineo-Congolian Region and Its Relationships to Other Phytocoria. *Bulletin du Jardin Botanique National de Belgique/Bulletin van Nationale Plantentuin van België* 49: 11–55.
- WHITE, F. 1983. The vegetation of Africa, a descriptive memoir to accompany the UNESCO/AETFAT/UNSO vegetation map of Africa, Paris.
- WIERINGA, J. J., AND M. S. M. SOSEF. 2011. The applicability of relative floristic resemblance to evaluate the conservation value of protected areas. *Plant Ecology and Evolution* 144: 242–248.

- A, J., J. J. LOUMETO, J. VOUIDIBIO, B. AMIAUD, AND D. EPRON. 2010. Influence du sol sur la répartition et la production de la phytomasse des savanes de la Cuvette congolaise. *Geo EcoTrop* 34: 63–74.
- YOKA, J., J. J. LOUMETO, J. VOUIDIBIO, AND D. EPRON. 2013. Productivité herbacée des savanes de la Cuvette congolaise (Congo-Brazzaville). *Afrique Science* 9: 89–101.
- ZALOUMIS, N. P., AND W. J. BOND. 2016. Reforestation or conservation? The attributes of old growth grasslands in South Africa. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 371(1703). 9 pages.
- ZANNE, A. E., G. LOPEZ-GONZALEZ, D. A. COOMES, J. ILIC, S. JANSEN, S. L. LEWIS, R. B. MILLER, N. G. SWENSON, M. C. WIEMANN, AND J. CHAVE. 2009. Global Wood Density Database. Dryad.